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A New Species of Raccoon, *Procyon garberi*, from Late Miocene (Late Hemphillian) Mehrten Formation, Stanislaus County, California

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Abstract.—The living raccoon, *Procyon lotor*, is a highly adaptable species inhabiting much of North America. Its evolutionary history, however, is poorly known due to a dearth of fossil records, especially pre-Pleistocene records. We describe a new species, *Procyon garberi*, from the late Miocene (late Hemphillian; approximately 6.4–6.2 Ma) Modesto Reservoir Member of the Mehrten Formation in the Modesto Reservoir area, Stanislaus County, California. This new species is relatively small among known species *Procyon*, and possesses primitive dental morphology, such as unwidened premolars, poorly developed posterior accessory cusp on p4, principal cusps in trigonid of m1 forming a high angle of 75–78°, and relatively long m2. However, limited and fragmentary materials from the Mehrten Formation make evaluations of the variations difficult in light of considerable size variations in living raccoon. Despite these difficulties, if we take the current fossil record at its face value, California has the earliest (late Miocene) and likely most primitive species in the form of *P. garberi*, followed by *P. rexroadensis* from the Pliocene (middle Blancan) of Kansas and Texas that has reached the living raccoon grade in dental morphology, followed by two species, *P. gipsoni* and *P. megalokolos*, in the early Pleistocene (late Blancan) of Florida, and by middle to late Pleistocene (Irvingtonian and Rancholabrean), *P. lotor* had emerged.

As a highly versatile omnivore, the common raccoon, *Procyon lotor* (Linnaeus, 1758), is the most successful species in the family Procyonidae and is ubiquitous throughout much of North America. With the exception of very high latitude northern Canada, high altitude Rocky Mountains, and arid deserts in part of Nevada, Utah, and Arizona, it seems that there is no terrestrial habitat that the raccoon cannot adapt to (Fig. 1). The history of the family Procyonidae can be traced to *Broili-ana* in early Miocene of Europe (Baskin 1982), or *Pseudobassar* in late Oligocene of Europe (Wang et al. 2023), but the majority of its fossil records are found in North America (Baskin 1982, 1989, 1998). Three species of the raccoons survive to the present day: North American common raccoon, *P. lotor*, Central and South American crab-eating raccoon, *P. cancrivorus*, and Cozumel Island dwarf raccoon, *P. pygmaeus* (Fig. 1). Recent molecular phylogenies estimated a divergence time of 25.71–32.12 Ma (Law et al. 2017) and ~20–30 Ma (Hassanin et al. 2021) for the family. For the genus *Procyon*, Koepfli et al. (2007) estimated a divergence time of 5.0–5.7 Ma.

Despite the modern success of *Procyon*, however, its early records are rare. Published fossil records include one species, *P. rexroadensis* Hibbard, 1941, from the Blancan (Pliocene) strata of Meade County, Kansas and Cita Canyon, Texas (Hibbard 1941; Oelrich 1953; Johnston and Savage 1955). Baskin (1982) mentioned a ?*Procyon* sp. in the latest Miocene of California. More recently Emmert and Short (2018) documented two early Pleistocene species, *P. gipsoni* and *P. megalokolos*, from Withlacoochee River 1A and Inglis 1A localities in central

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Fig. 1. Map of extinct species of *Procyon* (red, blue, and green labels and text) and living North American *P. lotor* (light shade of green), living Central and South American *P. cancrivorus* (light shade of yellow-brown), and Cozumel Island dwarf species *P. pygmaeus* (black arrow). Distribution for modern raccoons follows that of Lotze and Anderson (1979) for *P. lotor* and International Union for Conservation of Nature website¹ for *P. cancrivorus*.

Florida. All of above taxa were based on fragmentary materials. We describe a new species of *Procyon* from the late Miocene (late Hemphillian) Mehrten Formation in central California. This new species represents the earliest record of *Procyon* and sheds light on the origin, diversification, and early evolution of a very successful lineage.

Materials and Methods

Vertebrate fossils described in this paper are deposited in the Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County (LACM).

¹ Accessed at: <https://www.iucnredlist.org/species/41685/45216426>

Institutional Abbreviations.—**F:AM**, Frick Collection, American Museum of Natural History, New York; **KUVP**, Museum of Natural History, University of Kansas, Lawrence; **LACM**, Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles; **LACM M**, Department of Mammalogy, Natural History Museum of Los Angeles County, Los Angeles; **UF**, Museum of Natural History, University of Florida, Gainesville; **UM**, University of Michigan, Ann Arbor.

Systematic Paleontology

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Family Procyonidae Gray, 1825

Subfamily Procyoninae Gray, 1825

Procyon Storr, 1780

Type species.—*Ursus lotor* Linnaeus, 1758.

Included species.—*Procyon garberi* new species; *P. rexroadensis* Hibbard, 1941; *P. gipsoni* Emmert and Short, 2018; *P. megalokolos* Emmert and Short, 2018; *P. lotor* (Linnaeus, 1758); *P. cancrivorus* (Cuvier, 1798); and *P. pygmaeus* Merriam, 1901.

Diagnosis.—Short rostrum with anteroposteriorly shortened premolars; P1/p1 single rooted; P4 with a large hypocone and a very small metacone; M1 external cingulum reduced or absent; m1 with paraconid and metaconid close together; m2 elongate (modified from Baskin 1998).

Chronologic and geographic range.—Late Hemphillian to Present of North America and late Pleistocene to Present in South America.

Remarks.—In a series of papers, Baskin (1982, 1989, 1998, 2003, 2004) reviewed the systematics and phylogeny of Cenozoic procyonids, mostly placing *Nasua* Storr, 1780 and *Procyon* as sister taxa (plus other extinct stem taxa). From a modern procyonid perspective, Decker and Wozencraft (1991) proposed a phylogeny that also assumes a close relationship of *Nasua* (plus *Nasuella*) and *Procyon*, followed by *Bassariscus* Coues, 1887 at the base of their Procyoninae clade. A more exhaustive study of cranial and dental characters by Ahrens (2012) arrived at a somewhat different arrangement, but preserved the (*Procyon* (*Nasuella-Nasua*)) relationship. With the arrival of DNA sequences, the above morphological assessments are increasingly challenged by molecular studies that placed *Procyon* and *Bassariscus* as sister taxa (Fulton and Strobeck 2006; Koepfli et al. 2007; Eizirik et al. 2010; Koepfli et al. 2017) and isolate *Nasua* and *Nasuella* Hollister, 1915 in their own clade (Helgen et al. 2009; Helgen et al. 2013). If this is the case, our evaluations of character polarities and evolutionary trends assume that *Bassariscus* largely represents the ancestral conditions of the *Bassariscus-Procyon* clade.

Procyon garberi new species

(Table 2, Figs. 2–9)

Holotype.—LACM 62704, isolated left m1 and m2, presumably belonging to the same individual (Figs. 3, 6A–F), collected by Dennis Garber.

Type locality.—LACM locality 3942, Rhino Toe Island (Fig. 2), Modesto Reservoir Local Fauna, Modesto Reservoir Member of Mehrten Formation, Stanislaus County, California.

Etymology.—The species is named after Dennis Garber, who has amassed the largest vertebrate fossil collection from the Turlock Lake and Modesto Reservoir region. English translation: “Garber’s raccoon.”

Referred material.—From Modesto Reservoir Local Fauna, Mehrten Formation, Stanislaus County, California: LACM 62347, right dentary fragment with c-p1 alveoli and p2-4, LACM locality 3946, Modesto Reservoir no. 1 (Figs. 4, 6G, H), collected by Dennis Garber; LACM 162951, partial left dentary with c, p1 alveolus, p2-m1, and m2 alveolus, LACM locality 3942, Rhino Toe Island (Fig. 5), collected by Dennis Garber; F:AM 18114, right dentary fragment with C, p1 alveolus, p2-m1, and m2 alveolus, from Mt. Eden Local Fauna, Riverside County, California, late Hemphillian (Baskin 1982:figs. 12 B, D, 13) (Fig. 7).

Fauna, age relationship, and paleoenvironment.—VanderHoof (1933) was probably the first to report vertebrate fossils (an extinct horse *Pliohippus tantalus* Merriam, 1913) from near Oakdale in Stanislaus County, California. A ground sloth, *Megalonyx mathisi* Hirschfeld and Webb, 1938, was later described from Black Rascal Creek in “Upper Mehrten Formation” (Hirschfeld and Webb 1968:239). However, in an unpublished Ph.D. dissertation, Wagner (1981) conducted the first comprehensive geologic survey and worked out a biostratigraphic framework of the Mehrten Formation. Marchand and Wagner (1980) also produced a geologic map of the Turlock Lake Quadrangle. More recently, Sankey et al. (2015) reinvestigated the Turlock Lake fossil sites to place them in a modern geologic context (stratigraphic information archived in LACM and UCMP) (see also Sankey et al. 2016; Sankey and Biewer 2017).

Most of the vertebrate fauna from the Mehrten Formation, as defined in Wagner (1981), has not been published and only a few taxa are in the record: such as the giant “saber-toothed” salmon (fish) *Oncorhynchus* (*Smilodonichthys*) *rastrous* (Cavender and Miller, 1972) (Cavender and Miller 1972; Sankey et al. 2016), a cyprinid fish *Orthodon microlepidotus* (Ayres, 1854) (Casteel and Hutchison 1973), an extinct New World badger *Pliotaxidea garberi* Wagner, 1976, two plethodontid salamanders *Aneides lugubris* (Hallowell, 1849) and *Batrachoseps* sp. (Clark, 1985), and most recently, a giant tortoise *Hesperotestudo orthopygia* (Cope, 1878) (Biewer et al. 2014; Biewer et al. 2015; Biewer et al. 2016). Wang et al. (1999) and Tedford et al. (2009) listed several borophagine and canine canids from the Mehrten Formation without description or illustration. Balisi et al. (2018) did a systematic revision of Mehrten canids, recognizing four species: *Borophagus parvus* Wang et al., 1999, *B. secundus* (Matthew and Cook, 1909), *Vulpes stenognathus* Savage, 1941, and *Eucyon davisii* (Merriam, 1911). Most recently, Wang et al. (2018) described several well preserved coprolites, presumably excreted by *Borophagus parvus*, the most abundant bone-crushing canid in Mehrten Formation. These coprolites became the basis of a new ichnospecies *Borocoprois wangi* (Hunt and Lucas 2021).

Wagner (1976) published the first synthesis of regional strata and a biochronological evaluation for the Turlock Lake Local Fauna. Wagner (1981) later renamed this faunal unit Modesto Reservoir Local Fauna, a practice also followed by Clark (1985), Wang et al. (1999), Balisi et al. (2018), and Wang et al. (2018). We will follow this latter usage in the rest of this paper. A revised faunal list of the Modesto Reservoir Local Fauna is presented in Table 1. Wagner (1981) considered the upper portion of the Modesto Reservoir Member that contains the Modesto Reservoir Local Fauna to be equivalent in part with the Pinole Tuff and the Pinole Tuff Local Fauna in the San Francisco Bay area. The Pinole Tuff has been dated at 5.2 Ma (Evernden et al. 1964) and recalibrated to 5.3 Ma (Dalrymple 1979). Most recently, the Pinole Tuff Complex (and the Roblar Tuff within the former) has been newly dated to between 6.3-6.2 Ma by Wagner et al. (2021), which are more consistent with stratigraphic

Table 1. Faunal list of Modesto Reservoir Local Fauna from Modesto Reservoir Member of Mehrten Formation, based on Wagner (1976, 1981) (taxa that have no citation) and other publications (where a citation is provided).

Teleostei
Salmonidae
<i>Oncorhynchus (Smilodonichthys) rastrosus</i> (Sankey et al. 2016)
Cyprinidae
<i>Orthodon microlepidotus</i> (Casteel and Hutchison 1973)
Class Amphibia
Plethodontidae
<i>Aneides lugubris</i> (Clark 1985)
<i>Batrachoseps</i> sp. (Clark 1985)
Bufonidae
<i>Bufo</i> sp.
Ranidae
<i>Rana</i> sp.
Testudines
Testudinidae
<i>Hesperotestudo orthopygia</i> (Biewer et al. 2016)
Emydidae
<i>Clemmys</i> sp.
Squamata
Anguidae
<i>Gerrhonotus</i> sp.
Aves
Anatidae
<i>Branta</i> sp.
Lipotyphla
Soricidae
<i>Cryptotis</i> n. sp.
Talpidae
<i>Scalopoides</i> sp.
Xenarthra
Megalonychidae
<i>Megalonyx mathisi</i> (Hirschfeld and Webb 1968)
Lagomorpha
Leporidae
<i>Hypolagus</i> n. sp.
Rodentia
Sciuridae
<i>Spermophilus argonautus</i>
Geomyidae
<i>Parapliosacomys oregonensis</i>
Heteromyidae
<i>Perognathus mclaughlini</i>
Castoridae
<i>Castor</i> cf. <i>C. californicus</i>
<i>Dipoides vallicula</i>
Sigmodontinae
<i>Bensonomys</i> n. sp.
Cricetidae
<i>Paronychomys tuttlei</i>
Carnivora
Canidae
<i>Borophagus parvus</i> (Wang et al. 1999; Balisi et al. 2018)
<i>Borocopros wangi</i> (coprolite of <i>Borophagus parvus</i>) (Hunt and Lucas 2021)

Table 1. Continued.

<i>Borophagus secundus</i> (Wang et al. 1999; Balisi et al. 2018)
<i>Vulpes stenognathus</i> (Balisi et al. 2018)
<i>Eucyon davisii</i> (Tedford et al. 2009; Balisi et al. 2018)
Ursidae
Gen. et sp. indet.
Procyonidae
<i>Procyon garberi</i> n. sp. (this paper)
Mustelidae
<i>Plesiogulo</i> cf. <i>P. marshalli</i>
<i>Pliotaxidea garberi</i> (Wagner 1976)
<i>Galictis</i> n. sp.
Felidae
<i>Pseudaelurus hibbardi</i>
<i>Machairodus</i> cf. <i>M. catocopsis</i>
Proboscidea
Gomphotheriidae
Perissodactyla
Equidae
<i>Neohipparion</i> cf. <i>N. eurystyle</i>
<i>Nannippus</i> sp.
<i>Dinohippus interpolatus</i>
Rhinocerotidae
<i>Teleoceras</i> sp.
Artiodactyla
Tayassuidae
<i>Prosthennops serus</i> (= <i>kernensis</i>) (Prothero 2021)
Camelidae
<i>Procamelus</i> sp.
<i>Titanotylopus</i> sp.
<i>Hemiauchenia vera</i>
Palaeomerycidae
<i>Pedimeryx</i> cf. <i>P. hemphillensis</i>
Palaeomerycidae n. gen. and n. sp. 1
Palaeomerycidae n. gen. and n. sp. 2

superpositional relationships (Sarna-Wojcicki et al. 2021). This places the Modesto Reservoir Member in the late Miocene, not Pliocene, and places the Modesto Reservoir Local Fauna in the late to latest Hemphillian (Hh3-4) (Tedford et al. 2004). We consider the Modesto Reservoir Local Fauna to be approximately late Hemphillian (Hh3-4) in age between 6.4 and 6.2 Ma (Wang et al. 2018).

Axelrod (1980) listed 25 species of fossil plants from what he called Turlock Lake Flora consisting of 8 trees (including 1 conifer), 13 shrubs, 3 herbaceous perennials, and 1 or 2 vines. Of these, aquatic plants, such as *Cyperus* (flatsedges), *Juncus* (rushes), and *Typha* (cat-tails), are known to in the margins of streams, lakes, and ponds, and the plant-producing localities were envisioned to be lacustrine deposits “some distance from the shore” (Axelrod 1980, p. 89). Overall, the Turlock Lake Flora was characterized as an oak woodland-savanna and a floodplain assemblage, appropriate habitats for the new species of *Procyon* described herein.

Chronologic and geographic range.—Currently known from deposits of late Hemphillian age in California.

Diagnosis.—A small species of *Procyon*, about 25% (m1 length) to 14% (p4 length) smaller than the mean for *P. rexroadensis*. The trigonid of m1 is open with the angle

Table 2. Measurements (in mm) of lower teeth of *Procyon* species.

Taxa	Catal #	Source	c		p2		p3		p4		m1		m2	
			L	W	L	W	L	W	L	W	L	W	L	W
<i>P. garberi</i>	LACM 62347	This paper			4.99	2.53	5.65	3.08	6.95	3.55				
<i>P. garberi</i>	LACM 62704	This paper									9.83	5.04	9.49	5.03
<i>P. garberi</i>	LACM 162951	This paper	6.71	4.27	4.93	2.73	6.17	3.44	7.22	4.35	9.46	5.52		
<i>P. garberi</i>	F:AM 18114	This paper	7.13	5.43	5.44	3.30	6.17	3.69	7.85	4.44	10.34	5.42		
<i>P. rexroadensis</i>	UM 26997	Emmert & Short 2018							8.46	5.24	11.95	6.35	10.73	6.50
<i>P. rexroadensis</i>	UM 29646	Emmert & Short 2018							8.19	4.73	11.90	5.30	11.49	4.79
<i>P. gipsoni</i>	UF 243837	Emmert & Short 2018							8.37	6.17	11.15	7.22	10.59	6.86
<i>P. megalokolos</i>	UF 49251	Emmert & Short 2018							8.68	5.63	11.83	6.72		
<i>P. lotor</i>	LACM M54527	This paper	6.42	4.35	4.63	2.74	5.49	3.59	8.17	5.03	10.01	6.09	9.58	5.72
<i>P. lotor</i>	LACM M43542	This paper	7.04	4.81	4.67	2.84	5.01	3.45	8.02	5.50	9.82	6.02	9.97	5.93
<i>P. lotor</i>	Average (n=30)	Emmert & Short 2018							7.28	5.20	10.25	5.66	10.01	5.81
<i>P. cancrivorus</i>	Average (n=5)	Emmert & Short 2018							9.54	7.17	11.59	7.53	11.14	6.74

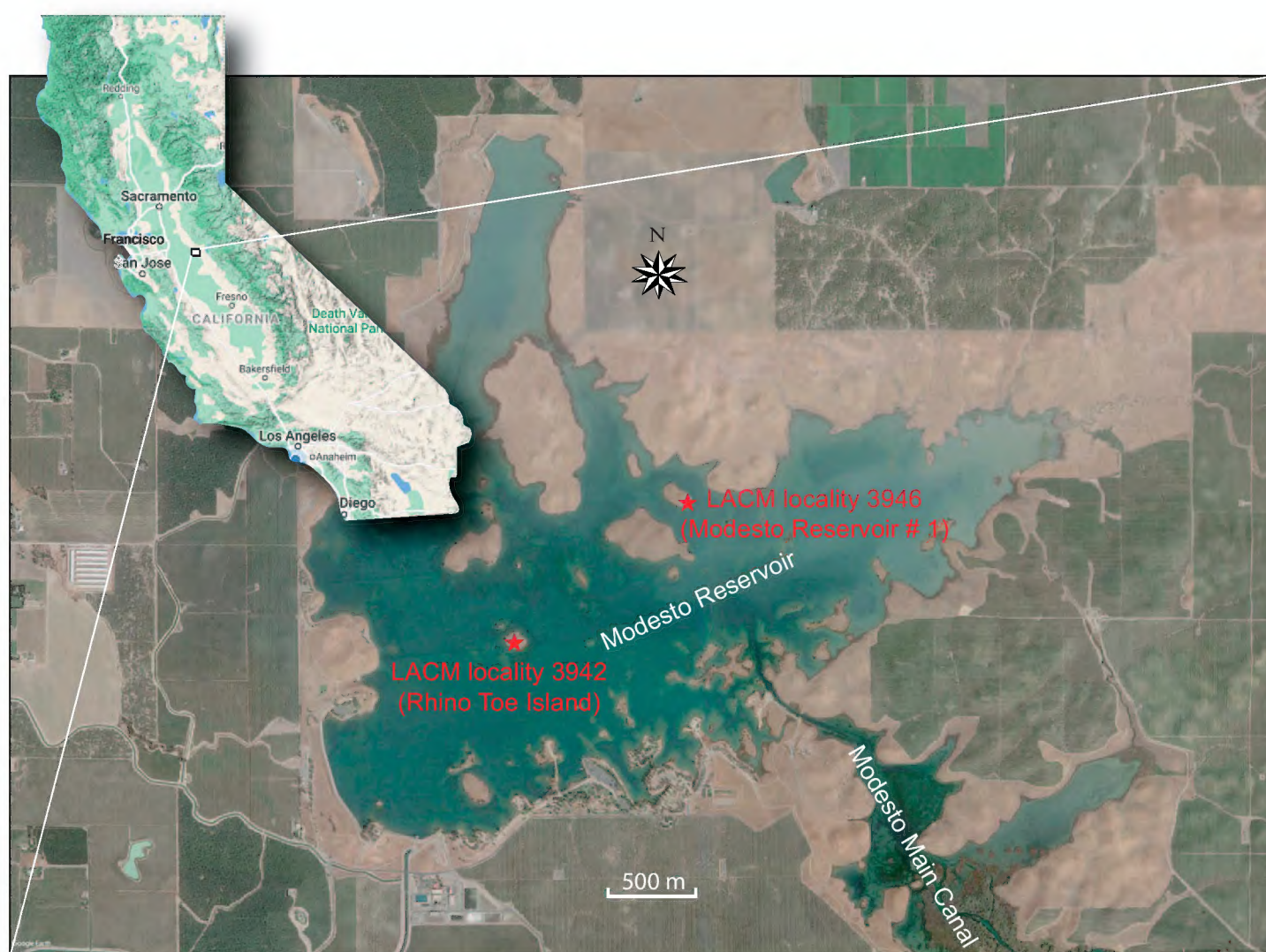


Fig. 2. Map of LACM localities 3942 and 3946 in Modesto Reservoir. Satellite images by Google Earth Pro (version 7.3.3.7786) (2023) was downloaded on 16 July 2021.

formed by the principal cusps of the trigonid being $75\text{--}78^\circ$. The m2 is long, as is for the genus. The p4 has a poorly developed posterior accessory cusp, differing from other species of *Procyon* and more closely resembling the condition found in *Bassariscus*.

Description.—Only portions of the lower dentition are preserved. It is possible to develop a composite description of the lower dentition for this taxon based on LACM 62347, 62704, and 162951. The lower canine is robust and has a slight backward hook, as in modern *Procyon*. The enamel surface lacks a shallow lateral groove seen in some individuals of modern raccoons. The p1 is a single-rooted tooth as indicated by the single alveolus present on LACM 62347 and 162951. The p2 is a robust, two-rooted, single-cusped tooth. The p3 is also single cusped, and has a slight posterior cingulum. The p4 is large; the main cusp is situated in its anterior portion, and is too worn to determine whether a posterior accessory cusp is present although it is likely absent. The p4 also lacks a lingual accessory cusp at the base of the main cusp seen in most living raccoons. A broad posterior cingulum is present but does not form a distinct cusp.

The m1 is a stout carnassial, with an open trigonid and a large talonid. The metaconid is a large cusp that may have been nearly equal in height to the protoconid, but due to wear it is not possible to determine this. The talonid is basined, with a cuspidate margin. The hypoconid is the highest cusp of the talonid. The entoconid and hypoconulid are nearly equal in height. A cusp anterior to the entoconid is present on the lingual margin of the talonid. This anterolingual cusp is separated from both the metaconid and entoconid. The talonid forms almost 50% of total length of the tooth.

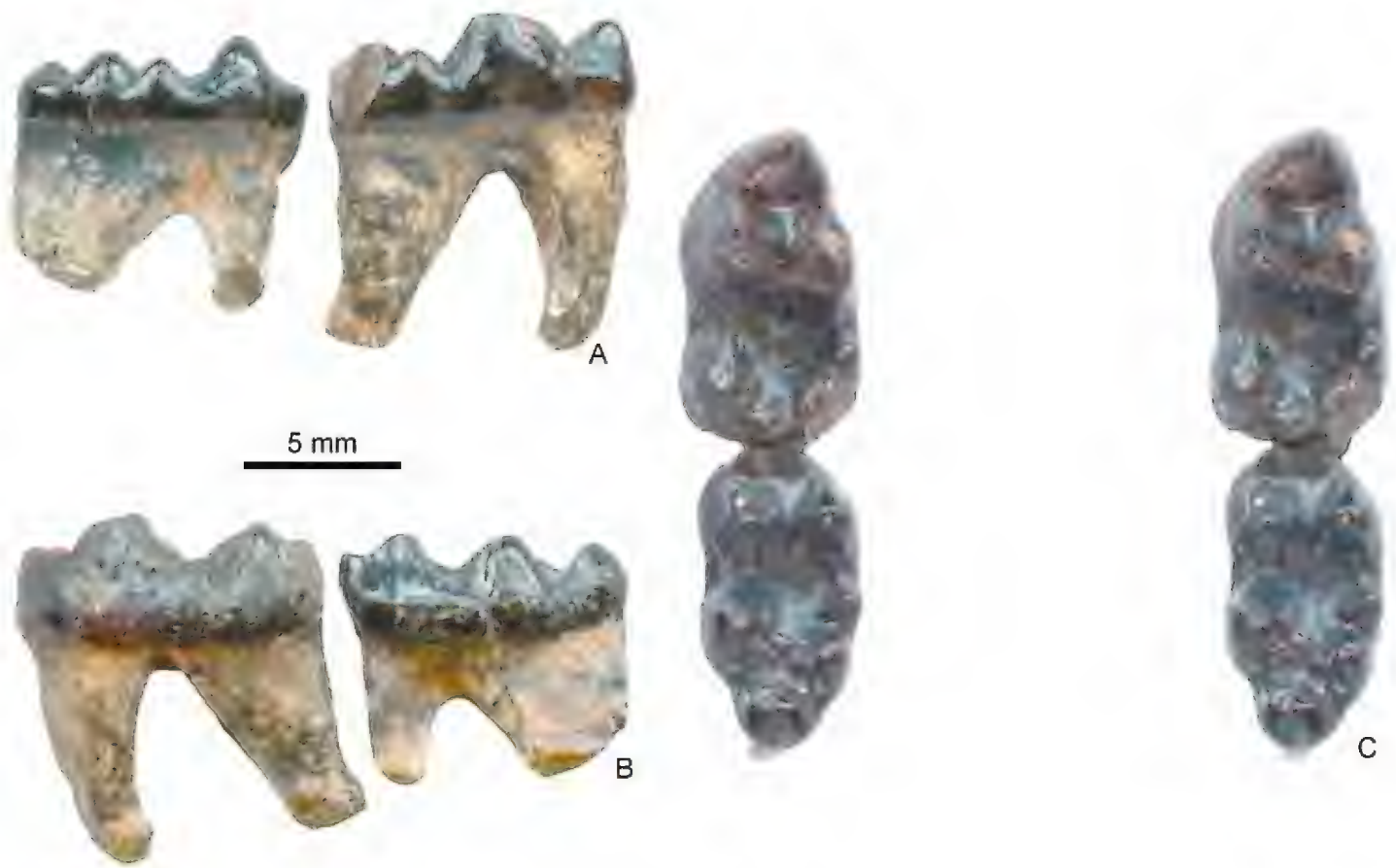


Fig. 3. *Procyon garberi*, n. sp., holotype, LACM 62704, LACM locality 3942, Modesto Reservoir Local Fauna, California, left m1-2; A, lingual view; B, labial view; and C, stereo photos of occlusal views.

The m2 is nearly equal in size to m1 (Table 2). The trigonid is small and the talonid large. The trigonid has a protoconid and metaconid, but only a small shelf is present where the paraconid would be. A small basin occurs between an anterior ridge and a crest formed between the protoconid and metaconid. The talonid is large and basined; the largest and highest cusp is



Fig. 4. *Procyon garberi*, LACM 62347, LACM locality 3946, Modesto Reservoir Local Fauna, California, right ramus fragment with p1 alveolus and p2-4; A, lingual view; B, labial view; and C, stereo photos of occlusal views.



Fig. 5. *Procyon garberi*, LACM 162951, LACM locality 3942, Rhino Toe Island, partial left ramus with c-m1 and alveoli of p1 and m2; A, stereo photos of occlusal view, B, lingual view, and C, labial view.

the hypoconid. The hypoconulid is well developed and forms a posterior lobe on the talonid. A well-developed entoconid is located anterior to the hypoconulid. Anterior to the entoconid is a cusp of nearly equal size. This cusp helps to close off the lingual margin of the talonid basin. Both m1 and m2 are two-rooted.

Comparison with known species of Procyon.—Baskin (1982:figs. 12 B, D, 13) figured a right ramus with c-m1 (F:AM 18114; Fig. 7) from Mt. Eden Local Fauna in southern California and tentatively called it “?*Procyon* sp.”, which was the oldest *Procyon* record then known. His main reason to include this specimen in *Procyon* is its anteroposterior shortening of premolars and relatively tall p2-3. Baskin’s measurements of the Mt. Eden specimen are consistent with those from Mehrten Formation. Heavy wear on LACM 62347 makes it difficult to directly compare the crown height between these two specimens, but the shortening of the premolars in F:AM 18114 seems to be slightly more advanced than the Mehrten form, especially in p3. Baskin’s descriptions of F:AM 18114 are minimal, and we tentatively refer this specimen to *P. garberi* pending availability of better materials.

Procyon garberi is a primitive species of *Procyon* based on the morphology of p4 and m1. *P. garberi* is considerably more primitive than *P. rexroadensis* Hibbard (1941) from the early Blacan Rexroad Local Fauna of Kansas and Cita Canyon, Texas (Johnston and Savage 1955). The holotype was based on an isolated left M1 (KUPV 5522), but was later supplemented with additional specimens, such as a nearly complete jaw (UM 26997) (Oelrich 1953). Morphologically, *P. rexroadensis* is very similar to the extant *P. lotor* and was, in fact, synonymized with the latter by Emmert and Short (2018) because it falls within the range of

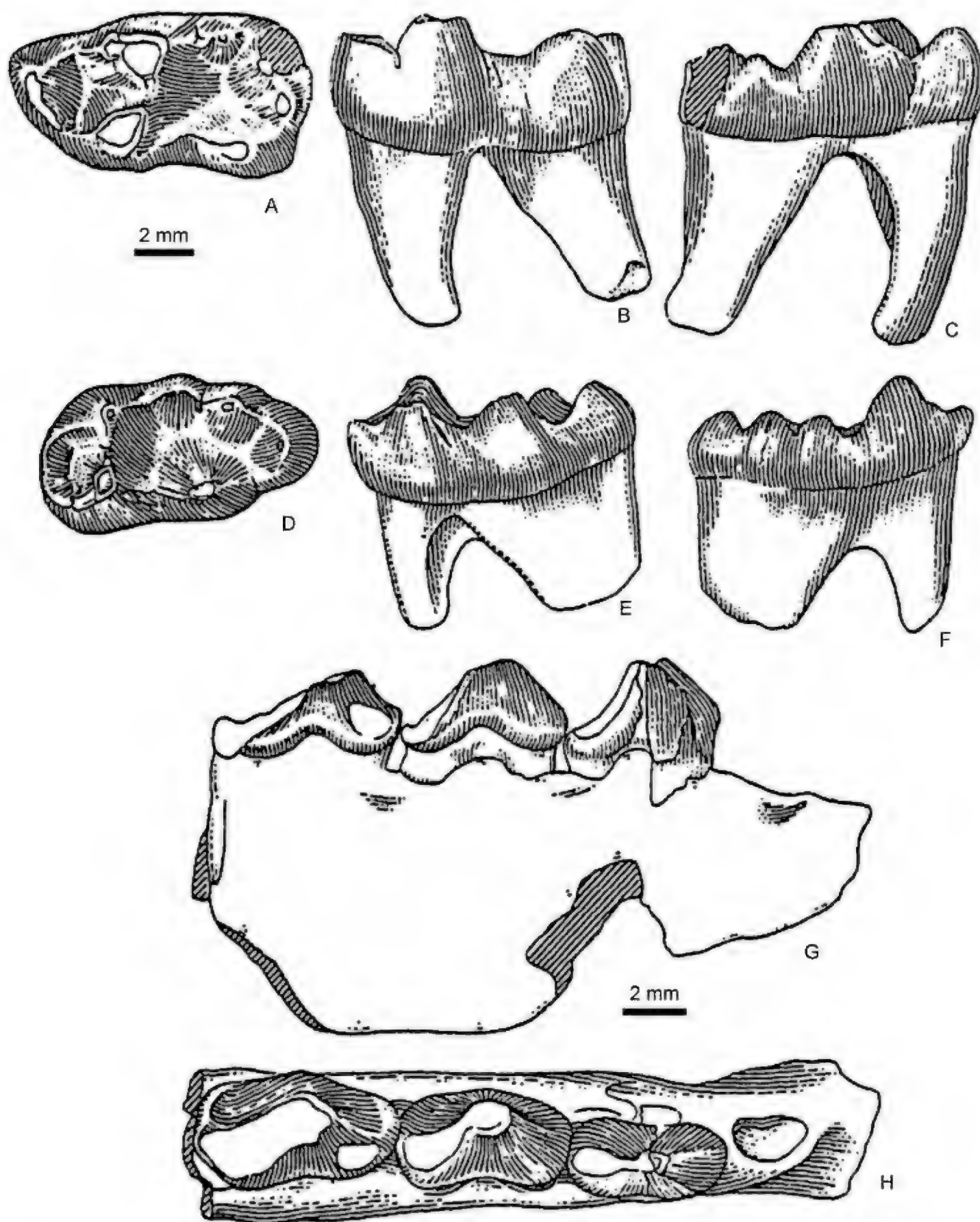


Fig. 6. *Procyon garberi*, n. sp., holotype, LACM 62704, LACM locality 3942, Modesto Reservoir Local Fauna, California, left m1, m2; A, left m1, occlusal view; B, left m1, labial view; C, left m1, lingual view; D, left m2, occlusal view; E, left m2, labial view; F, left m2, lingual view. LACM 62347, LACM locality 3946, right dentary fragment with p2-4; G, labial view; H, occlusal view. Illustration by Mrs. Jaime Pat Lufkin.

variations in living *P. lotor*. Despite this difficulty in diagnosing it, *P. rexroadensis* may serve as a chronospecies in the Pliocene of the Great Plains pending future discoveries (this species is still poorly known, thus the limited characters in diagnosing it). We also note that *P. rexroadensis* falls in the high ends of m1 measurements of *P. lotor* and it has relatively narrower m1 (Fig. 8). Regardless of its taxonomic status, *P. rexroadensis* is useful as a point of comparison



Fig. 7. *Procyon garberi*, referred specimen, F:AM 18114, from Mount Eden Local Fauna, Riverside County, California, partial right dentary with c, p1 alveolus, p2-m1, m2 alveolus; A, occlusal view; B, lingual view; C, labial view. Photos courtesy of Qigao Jiangzuo.

because it has achieved the trigonid morphology of m1 characteristic of *Procyon* that persists in the subsequent fossil and extant species of the genus. Yet it differs from that of *P. garberi* from the late Miocene.

The relationships of the length of m1 to the length of m2 (Table 2) and the width of the trigonid of m1 to the width of the talonid of m1 were examined to determine if any primitive versus advanced character patterns were apparent within the genus *Procyon* and with other genera of procyonids. *Procyon garberi* differs markedly from *P. rexroadensis* and *P. lotor* in the morphology of p4 and m1. In the latter two species, the posterolabial region of p4 is greatly expanded and the posterior accessory cusp is large and located labially to the protoconid. In *P. garberi* there is no evidence of the posterolabial expansion of the posterior region of this tooth. The posterior accessory cusp in *P. garberi*, if present at all, is less well developed as in the other two species.

The morphology of m1 in *Procyon garberi* is more primitive than found in any other species of *Procyon*. In *P. garberi*, the angle formed by the cusps of the trigonid is 75-78° (Fig. 9). Although such a measurement may be difficult to define in worn specimens, it serves as an approximate guide for how “closed” the trigonid is. In the extant *P. lotor* this angle is, on the average, 60° (Fig. 9). In the extinct *P. rexroadensis*, it is 62°. The high angle (75-78°) found in *P. garberi* more closely resembles that found in *Bassariscus astutus* (Lichtenstein, 1830), where it averages 84° and *B. sumichrasti* (Saussure, 1860) where it averages 70°. The high

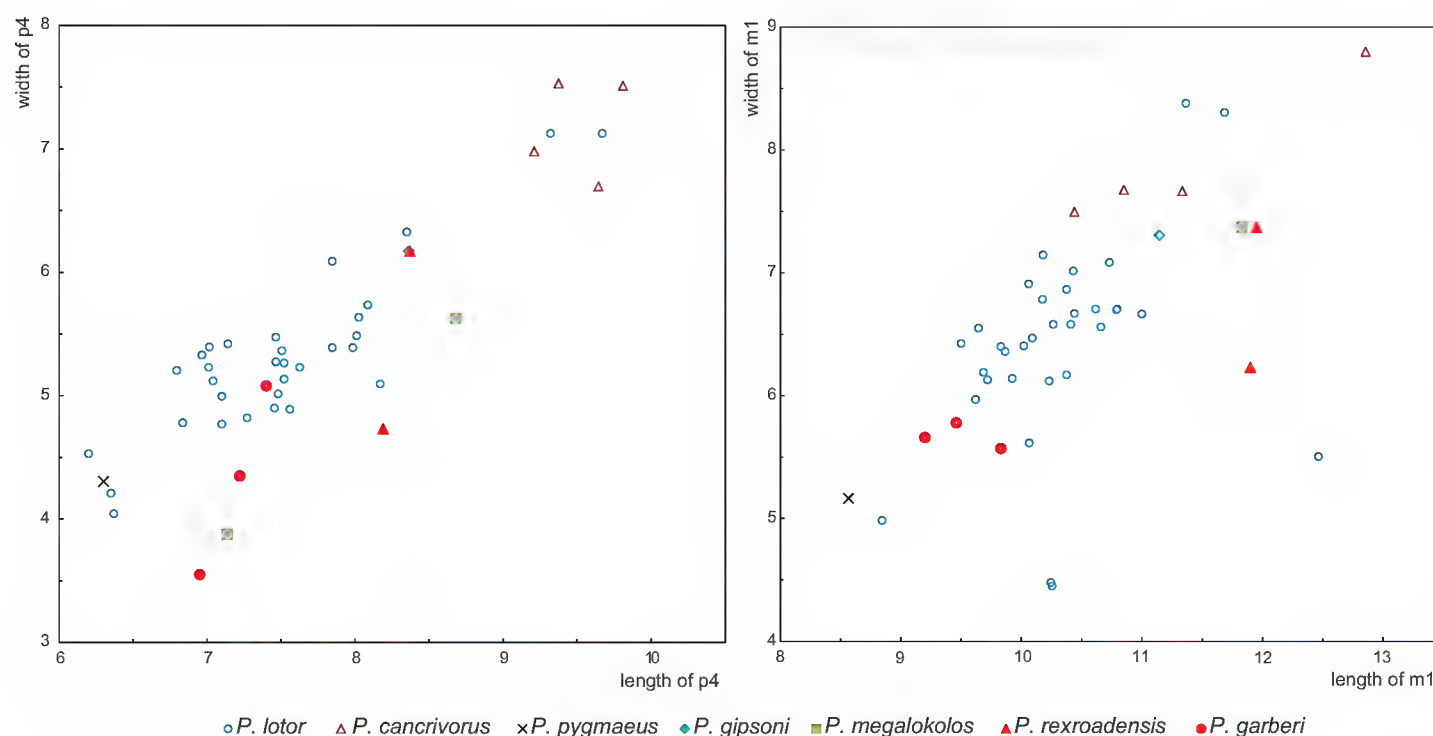


Fig. 8. Bivariate plots of p4 (left) and m1 (right) lengths and widths. Measurements for modern species of *Procyon* and Florida Pleistocene species are courtesy of Laura G. Emmert; see Emmert and Short (2018) and Gilmore (2013) for sources of specimens.

angle is considered a primitive character for *P. garberi*, not yet reduced to the extent found in the other species of *Procyon*. If it were not for the highly modified m2 of *P. garberi*, which very closely resembles that of the other species of *Procyon*, the m1 of *P. garberi* would be sufficiently distinctive that this species would not be considered as belonging to the genus *Procyon*, but to some procyonid intermediate between *Bassariscus* and *Procyon*.

The m1/m2 ratios we recorded basically show that in size and development of m2, *P. garberi* was as advanced as other species of *Procyon*. Likewise, the development of m1 was similar to other species of *Procyon*. The relationship of the width of the trigonid of m1 to the width of the talonid of m1 demonstrated that there was considerable variation within the genus *Procyon*, and that *P. garberi* fell within the variation found between *P. lotor* and *P. cancrivorus*.

Baskin (1998) listed additional North American localities that produced “*Procyon* sp.”: from Florida: latest Hemphillian Upper Bone Valley Fauna (GC13B); late Blancan Santa Fe River 1A and 1B sites (GC14); late Blancan St. Petersburg Times site (GC16); late Blancan Pinecrest beds (GC17); from California: Irvingtonian Anza-Borrego site, Palm Springs Formation (NB13C); and from Washington: late Blancan Ringold Formation (PN4). Although suggesting far wider distributions than is discussed here, most of these records exist in faunal lists and we did not have the opportunity to examine them.

Emmert and Short (2018) recently described two new species of *Procyon*, *P. gipsoni* and *P. megalokolos*, and one new species of *Nasua*, *N. mastodonta*, from various late Blancan sites in Florida, which were based on the senior author’s unpublished Master’s thesis (Gilmore 2013). Both these early Pleistocene species of *Procyon* are either slightly or significantly larger than living *P. lotor*, in addition to other unique morphologic characters of their own. Most of their diagnostic characters of these new species can be equally applied to *P. garberi*, where comparable materials are available.

Discussion

Fragmentary jaws and teeth for *Procyon garberi* prevent an evaluation of its size and morphological variations. Such a poor knowledge also hinders a detailed phylogenetic analysis.

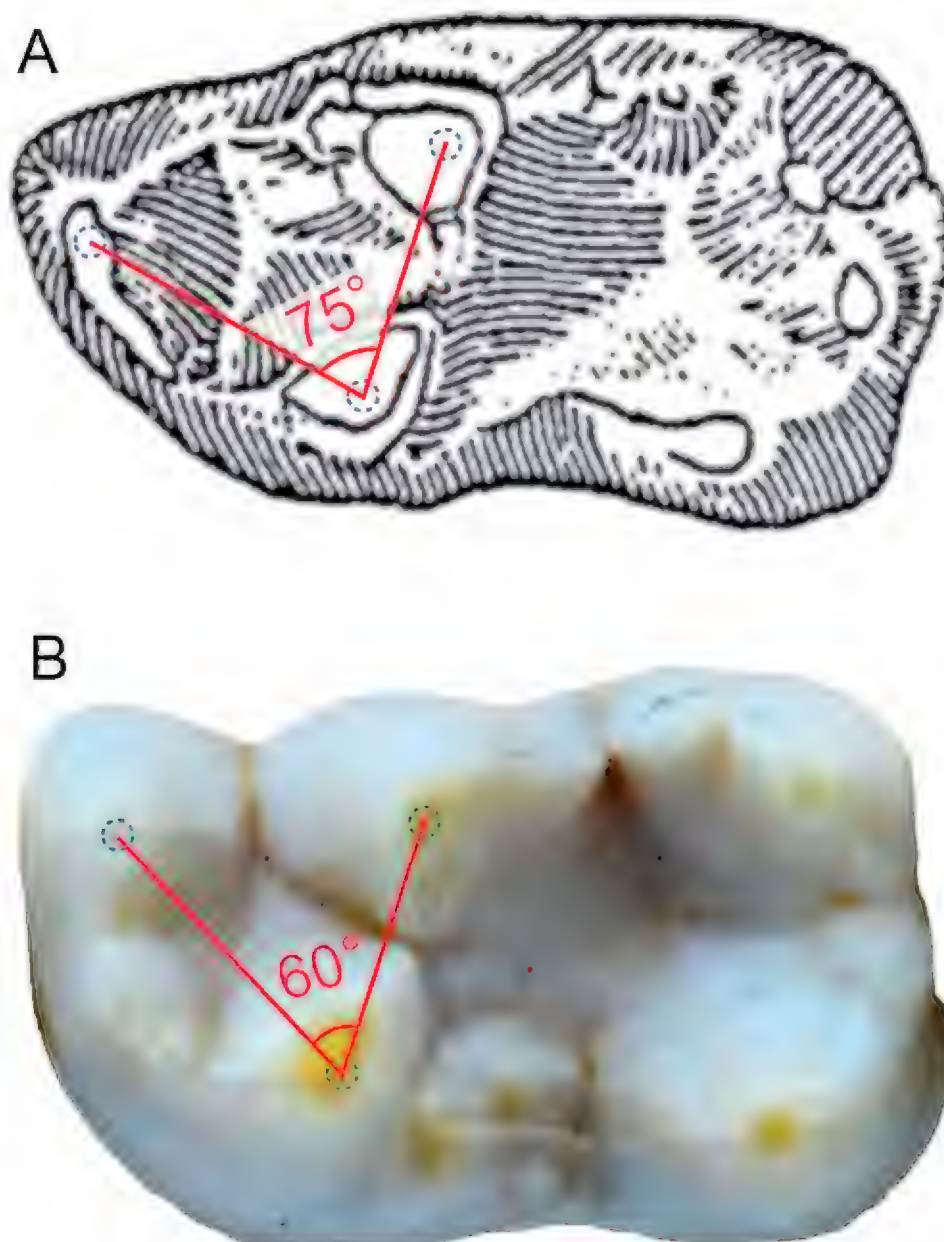


Fig. 9. Comparison of m1 trigonid cusp angles; A, *Procyon garberi*, LACM 62704; B, *Procyon lotor*, LACM (M) 43542, mirrored from that of the right. See text for discussions.

Nevertheless, it appears that *Procyon garberi* is a primitive species of *Procyon* that may not have been ancestral to the lineage leading directly to *P. lotor*. *P. rexroadensis* in the early Blancan Rexroad Local Fauna is so close to *P. lotor* as to be nearly indistinguishable, and this suggests that *P. garberi* probably is an early primitive species of *Procyon* that appeared along the west coast of North America in late Hemphillian time.

Our examination of the extant Nearctic procyonids indicates that living *Bassariscus* possesses the most primitive characteristics of the family Procyonidae, based upon dental morphology, primarily that of m1. *B. sumichrasti* appears to more closely related to the other Nearctic forms than does *B. astutus*. *B. sumichrasti* possesses the characteristics of m1 that would allow for the derivation of *Procyon* and *Nasua*, *Bassaricyon* and *Potos*, rather than *Bassariscus astutus* since the angle formed by the cusps of the trigonid in *B. sumichrasti* shows closure not apparent in the other species of *Bassariscus*. It is apparent that *Nasua* and *Procyon* share the most dental characteristics in their m1 and m2, as also suggested by most morphological and paleontological studies (Baskin 1982, 1989; Decker and Wozencraft 1991; Baskin 1998; Ahrens 2012), but if recent molecular studies indicate the true relationships (Fulton and Strobeck 2006; Koepfli et al. 2007; Eizirik et al. 2010; Koepfli et al. 2017), some of these shared characters are likely due to convergences.

Our knowledge about the early evolution of *Procyon* is still very limited, especially in the Miocene to Pliocene records (Fig. 10). Based on known materials, *Procyon* originated in or close to the

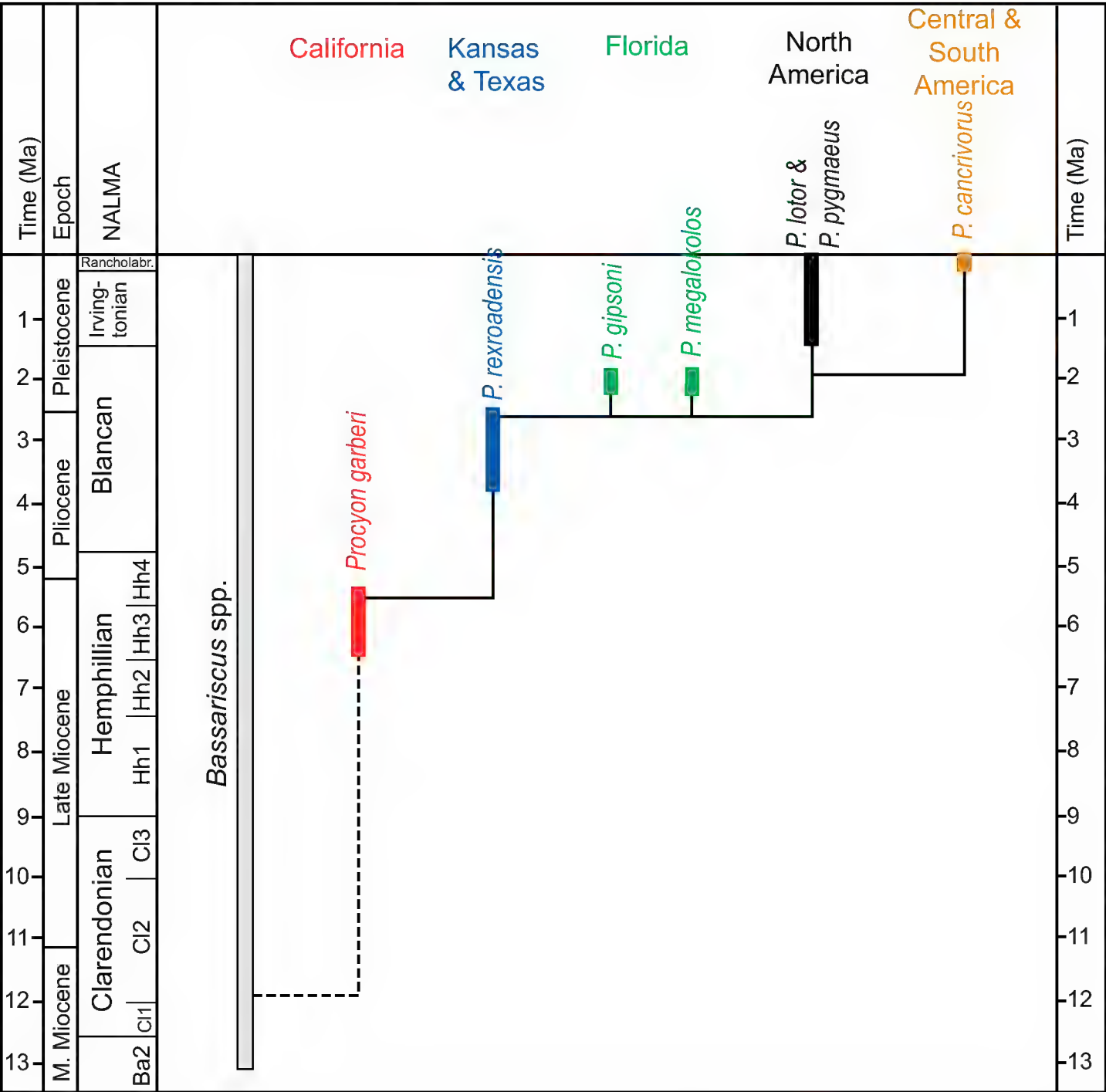


Fig. 10. Chronologic range of species of *Procyon*. We follow Arata and Hutchison (1964) and Emmert and Short (2018) in synonymizing previously named middle to late Pleistocene species (such as *P. priscus* Leidy, 1856; *P. simus* Gidley, 1906; *P. nanus* Simpson, 1929) as *P. lotor*. South American records of *Procyon* follow those by Soibelzon (2011) and Ruiz-Ramoni et al. (2018). Chronological ranges for North American Land Mammal ages follow Tedford et al. (2004) and Bell et al. (2004). We adopt 2.58 Ma as the beginning of the Pleistocene Epoch, as ratified by the International Union of Geological Sciences (IUGS) (Gibbard et al. 2010).

west coast of North America during the late Miocene (late Hemphillian) in the form of *P. garberi*. The next records are found in the Pliocene (middle Blancan) of the Great Plains (Kansas and Texas) in the form of *P. rexroadensis*. By the Pliocene, dental morphology of *Procyon* has reached the modern raccoon grade. By the early Pleistocene (late Blancan), two new species were documented in Florida, but these appeared to be not in direct line of descent to living raccoons. From the middle Pleistocene (Irvingtonian) to Present, all North American records are identifiable to *P. lotor*.

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Did Post-Drought Storm Events Trigger Long-Distance Coastal Dispersal of an American Beaver in Coastal Southern California?

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The American Beaver *Castor canadensis* typically occupies freshwater habitats, but in some areas the species occurs in estuaries, lagoons, tidal marshes, and coastal floodplains (Pasternack et al. 2000; Hood 2012; Goldfarb 2019). Both *C. canadensis* and the Eurasian beaver *Castor fiber* disperse in salt water to colonize new territories (Anderson et al. 2009; Halley et al. 2013; Curley et al. 2019), yet little is known about the frequency, distances, and survivorship of such events. In some cases, the distances appear to be considerable (Pietrek and González-Roglich 2015). For example, *C. canadensis* rapidly spread across Tierra del Fuego, Chile, after being introduced to the island by humans in 1946, then eventually crossed the Beagle Channel (~5 km wide at its narrowest point) to occupy adjacent islands to the south (e.g., Islas Navarino, Hoste, Picton, Nueva, and Lennox) before advancing westward across the Strait of Magellan via Isla Dawson (~10 km at the narrowest point) to invade the Patagonian mainland (reviewed in Anderson et al. 2009; Pietrek et al. 2017; Huertas Herrera et al. 2020). Beavers have also dispersed to nearshore islands in Canada (Naughton 2012), have successfully colonized insular Newfoundland and Labrador (Curley et al. 2019), and have been documented anecdotally from Isle au Haut more than 11 km off the coast of Maine in the eastern United States.¹

We report on a dead *C. canadensis* recovered inside Mission Bay in San Diego County, California USA on 07 April 2017. The location of the beaver within a metropolitan area less than 7 km (airline) from downtown San Diego was highly unusual, as the closest sites occupied by *C. canadensis* are ~62 km (shoreline contour) to the north in the Santa Margarita River (Fig. 1), where the species was introduced in the 1950s (Lang et al. 1998; Hunsaker 1992). The beaver, estimated to be an 18–23 kg adult (so large that it required two San Diego County Park Rangers to lift it into the bed of a pickup truck), was recovered at the back of the bay adjacent to the California Interstate 5 freeway, opposite of the bay's inlet (Fig. 1b). The specimen was disposed of before it was brought to the attention of local biologists, but details of its disposition were made from direct observations by San Diego County Park Ranger Sylvia Sowadski, who was dispatched to the scene and photographed the animal in situ (Fig. 2). San Diego County Park Rangers often assist with the recovery of animal carcasses, as wildlife mortality is a common occurrence due to the location of Mission Bay within a heavily urbanized area (S. Sowadski pers. comm. 2022). Aside from mild bloating, the beaver showed no signs of trauma and was in good condition at the time of discovery (i.e., no foul odor, leaking fluids, wounds, obvious necrotic tissue, etc.), consistent with a recent death (S. Sowadski pers. comm. 2022).

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¹ <https://acadiaonmymind.com/2015/08/beaver-in-acadia-national-park>.



Fig. 1. Location of the Mission Bay beaver (San Diego County, California) and its putative site of origin in the Santa Margarita River. a.) Southern extension of the Southern California/Northern Baja California coast ecoregion and subregions showing the major coastal drainages of San Diego County [subregions a–c and northern Baja California not shown (map adapted from Griffith et al. 2016)]. b.) Aerial view of Mission Bay (Google Earth image), with the red bullet indicating the beaver’s location. The highway running north/south on the right (east) side of the map is CA Interstate 5.



Fig. 2. Deceased adult *Castor canadensis* recovered from Mission Bay, San Diego County, California USA. Photo by San Diego County Park Ranger Sylvia Sowadski.

While the cause of death is unknown, hypernatremia may have been one of several contributing factors, because *C. canadensis* lacks specialized excretory systems to mitigate electrolyte imbalance and or dehydration in high salt conditions (Strules and DeStefano 2015). Beavers occupying intertidal habitat farther north along the Pacific Coast are sometimes found dead or dying on shorelines due to excess sodium intake,² a pattern that fits with the observation here for Mission Bay. The Mission Bay beaver also appeared to be bloated at the time of its recovery (Fig. 2), a common sign of water retention caused by salt imbalance (Peng et al. 2019). Other possible causes of death include being struck by a boat or other watercraft, although the absence of any obvious outward trauma suggests otherwise.

The underlying cause of how and why the beaver ended up in Mission Bay cannot be known, but the incident occurred in the wake of severe, atmospheric river-enhanced Pacific storms that marked the end of California's most severe drought on record (Wang et al. 2017). Surficial flows for the Santa Margarita River, the presumptive source of the beaver, were exceptional after the 2012–2016 drought and may have been significant enough to displace the beaver or stimulate this atypical behavior (Fig. 3). Heavy precipitation was concentrated into four periods during the first two months of 2017, with the Santa Margarita River rising nearly 3.0 m (~10 ft) over a 24-hr period to a height of 4.5 m (or 14.6 ft, almost four feet above the flood stage of 10.8 ft) on January 23rd, and flow rates reaching as high as 883.15 m³/s (31,188 ft³/s) (U.S. Geological Survey, gauge no. 11046000 at Ysidora, California, the most downstream gauge station on the Santa Margarita River, U.S. Geological Survey 2022; Fig. 3). These events were capped by an intense, final storm on 27 Feb 2017, with precipitation amounts ranging from 5.1–10.2 cm (2–4 in) along the coast to 10.2–20.3 cm (4–8 in) in the western foothills of the Laguna Mountains, causing severe flooding across parts of San Diego County.³

Intermittent, volatile storm flows are known to breach the dams of *C. canadensis* from coastal streams north of Point Conception in Santa Barbara County (Swift et al. 1997), and beavers have been documented in the brackish lagoons at San Mateo Creek and the Santa Margarita

² Goldfarb, B. 2019. The gnawing question of saltwater beavers. Hakai Magazine, Victoria, British Columbia. Retrieved from <https://hakaimagazine.com/features/the-gnawing-question-of-saltwater-beavers/>.

³ summary data accessed from <https://www.cnrfc.noaa.gov>.

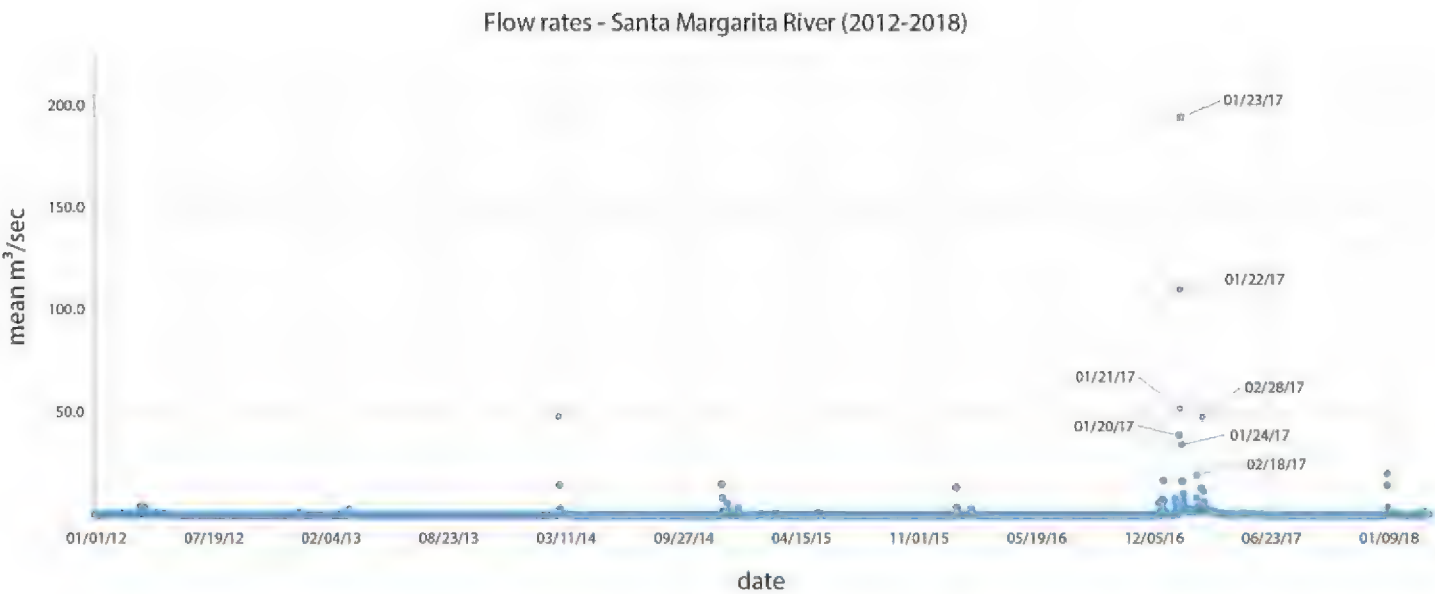


Fig. 3. Flow rates for the Santa Margarita River from January 2012–2018 (U.S. Geological Survey 2022). California’s megadrought began in 2012 and was declared over following atmospheric-river enhanced storms in early 2017 (Wang et al. 2017).

River (Woefel 1991; Holland and Swift 2000: Fig. 1a). Although this individual’s motivation for leaving the Santa Margarita River is unknown, the sudden high volume and rapid flows caused by the 2017 post-drought storms, coupled with decreased salinity in the lagoon and near-shore areas, may have coaxed the animal into dispersing outside of the lagoon. Freshwater discharge during and after extreme storm events decreases nearshore salinity along the California coastline (Warrick et al. 2007; Lahet and Stramski 2010; Cheng et al. 2016) and may have created conditions that were less hypertonic to the animal, and therefore more favorable for marine dispersal. In fact, salinities following atmospheric river-related storms in coastal California reach concentrations that are low and long enough in duration to cause mass mortality events in the Olympia Oyster (*Ostrea lurida*) (Cheng et al. 2016). Longshore currents pushing southward along the southern California coastline also strengthen during the winter months due to swells originating out of the Gulf of Alaska (Winant and Bratkovich 1981; Di Lorenzo 2003), and are consistent with the beaver’s direction of movement.

Given that several estuaries exist between the Santa Margarita River and Mission Bay (Fig. 1a), it is unclear why the beaver would have traveled so far south before moving inland, whether it did so incrementally, and whether it made the trek exclusively in the ocean. Some of the distance may have been covered by movement along coastal beaches or other terrestrial habitat, as beavers are known move considerable distances over land (reviewed in Pietrek et al. 2017). They also tend to disperse farther in situations where there are no potential mates close by or habitat quality is subpar (Altwegg et al. 2013; Pietrek and González-Roglich 2015). No other beavers were reported outside of the Santa Margarita River during this time period, although others may have engaged in similar behavior but were undetected.

Given its fresh condition, absence of outward trauma, and interior location within Mission Bay, it is possible that the beaver was searching for a way out of saline conditions. Freshwater inputs from Tecolote Creek and Rose Creek, which would have been flowing during this period of storm activity, lead to lower salinities toward the back of the bay during the rainy season, particularly after large storms (Elliott and Kaufmann 2007; Talley et al. 2015). At the front of the bay, the ocean inlet is artificially separated from the adjacent mouth of the San Diego River by a seawall – once inside the seawall, the beaver would have been guided into Mission Bay and had no chance to disperse up the San Diego River without crossing a heavily

trafficked four-lane road (Fig. 1b). The likelihood that this individual used either Tecolote or Rose Creek as an entry point is low given the network of freeways and other urban development surrounding both drainages, and there are no beaver-occupied sites in the adjacent San Diego River.

Whether the beaver was dead or alive when it entered Mission Bay cannot be known, but the recovery site and other anecdotal evidence suggests it was alive. Had it died outside the bay and entered from the ocean, it is unlikely that waif dispersal alone could explain the animal's location given the convoluted shoreline and the position of two islands (i.e., Vacation Isle and Fiesta Island: Fig. 1b), which would have presented obstacles to a drifting carcass. A study of surface water movement in Mission Bay showed that drift tubes released near the inlet almost never made it to the back of the bay where the carcass was found (Levin 1983), further suggesting that passive transport was unlikely. Last, the in situ photo of the beaver shows movement of the hands and tail in the sand and possible footprints behind the tail, although higher tide water could have agitated the limbs to create these impressions (Fig. 2).

We explored the possibility that this individual was a fugitive from Sea World San Diego (a marine mammal-focused theme park, oceanarium, and aquarium), which is located along the southern edge of Mission Bay, but the one beaver that has ever resided at Sea World was transferred permanently to the San Diego Zoo well before 2017. The only other explanation could be that the animal was intentionally trapped, transported, and released or discarded by humans in one of the most heavily urbanized parts of the county, which seems highly improbable but cannot be ruled out. While the lone seafarer reported here may be an anomaly, this observation combined with previous records in the lagoons at San Mateo Creek and the Santa Margarita River, demonstrate the potential for beavers to disperse into unoccupied watersheds in San Diego County, and that individuals may be more likely to do so after periods of exceptional rainfall.

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Jaguar (*Panthera onca*) in California: A History and a Future

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Reintroduction of large carnivores to regions they once inhabited has been considered or implemented for many species in North America, including gray wolf (*Canis lupus*), red wolf (*C. rufus*), grizzly bear (*Ursus arctos*) and others (Fritts et al. 1997; Merrill et al. 1999; Maehr et al. 2001; Phillips et al. 2003; Smith 2003). Reintroduction of large apex predators comes with significant potential risks—not only to the species being restored, but to the contemporary ecosystem (Smith and Peterson 2021; Baker et al. 2017) and to the public (Carroll et al. 2001). The counter argument is that such programs can in fact have beneficial effects on ecosystem health, ecotourism, and wide-ranging predator-prey interactions as well as other ecological processes (Ripple and Beschta 2003; Marshall et al. 2013; Martone et al. 2020; Smith et al. 2020). Additional consideration has been placed on peripheral populations, which would be classified as “non-essential experimental populations” by the United States Fish and Wildlife Service, that could be managed in the United States (Lesica and Allendorf 1995; Sanderson et al. 2021). Potential risks and benefits of restoring large predators in their ancient territories must be weighed very carefully (Baker et al. 2017; Maehr et al. 2001; Clark et al. 2005; Sanderson et al. 2021), and great consideration must be given to the anticipated welfare and success of the species itself.

A number of factors come into play: Is the habitat currently intact, and does it afford the species opportunities to grow in distribution and connect with other (reintroduced or naturally occurring) populations (Abbitt et al. 2000)? Are the risk factors associated with a large human population likely to result in negative outcomes (Clark et al. 2005; Lee et al. 2021)? Among myriad questions to be considered, the temporal scale of the proposed restoration is particularly critical. Is the intent of restoration to reintroduce keystone, preexisting species from a particular period (e.g., species present before European settlement)? Is the intent to restore an ecological unit (ecosystem, biological province, or other large-scale biotic unit) to a condition conducive to the reintroduced species? Or is it simply to restore a focal species and its prey base “because we can,” without regard to the contemporary environment (Callicott 2011a)? Callicott (2011b) proposed that environmental timescale—that is, habitat- and condition-based restoration to a preexisting baseline—is the aspiration likeliest to succeed, laying as it does the groundwork for reintroduction of a species based on its known past occurrence and ecosystem needs. Restoration teams can then elect reintroduction goals based on evidence gleaned from historical or prehistoric presence. In such efforts, understanding the verifiable past range of a species assumes immense importance (Wolf and Ripple 2018).

Scientific literature has contributed significantly to establishing the known past occurrence and range of species; these data and observations are ideal for establishing goals for environmental restoration to conditions present at a particular period in the past (Redford et al. 2011). If a temporal framework is the goal, an understanding of the distribution during certain time events may be critical. Van Vuren and Deitz (1993) reported evidence of former occurrence of bison (*Bison bison*) in central and northeast Nevada, noting that such evidence can inform our understanding of the species’ historical context. This, in turn, might suggest the likelihood of the species’ successful reintroduction should conditions be reproducible for the long term.

Storer and Tevis (1955) reviewed the history of grizzly bears (*U. arctos horribilis*) in California, including information about occupied habitats and the historic distribution. Their well considered findings suggested the reproducibility of conditions conducive to grizzlies should the species be reintroduced. In an attempt to establish the historical range of the California condor (*Gymnogyps californianus*) on the Pacific Coast over time, D'Elia and Haig (2013) consulted 81 records, including anecdotal accounts, letters, journals, newspaper articles, the feathers on an indigenous costume, and museum specimens dating back to 1805. Their data pointed to a steep decline in condor populations after European settlement in the state, suggesting that a species restoration plan would need to give careful consideration not only to reproducibility of historical environmental conditions, but to protection from human activity. Such a program was initiated and is showing promising results in restoration and protection of *G. californianus* populations on the Central Coast (Kelly et al. 2015). Data can also be used to support or discourage species reintroduction and restoration. For example, Ripple and Beschta (2003) looked at the history of cougars (*Puma concolor*) in Wyoming's Yellowstone National Park, and determined, through an in-depth investigation of anecdotal records and letters, historical photographs, and trapping data, that current numbers of cougars were likely higher than historical numbers in that area. In such a situation, species restoration or population augmentation would presumably be unwarranted. It is important to note that indication of past and potential future occurrence of a species in an area is just that, support for assessing reintroduction. These data do not address the advisability of such reintroductions.

Reestablishment of jaguar (*Panthera onca*) in western North America has recently come under discussion. The species contemporary occupation of portions of Arizona and New Mexico (migrating individuals from Mexico) prompted the listing of *P. onca*, in the United States, as an endangered species under the Endangered Species Act (ESA)(USFWS 1997). The elevation in federal status precipitated discussions related to augmentation of colonizing populations, and potential reintroductions (Povilitis 2015; Sanderson et al. 2021). Although Povilitis (2015) has advocated for population restoration (both augmentation and reintroduction), others are in support of peripheral populations that can be managed in a different manner (Gittleman et al. 2001; Nielsen et al. 2001; Wolf and Ripple 2018) from that set forth by the Jaguar Recovery Plan (USFWS 2018). Hayward et al. (2007) noted that when introductions are planned, they should occur within the known historical range from which the species was extirpated.

It is also noteworthy that, although the historical data can provide a context for future management, research, or reintroductions, their reliability must be viewed with caution (Adams et al. 2023). Ripple and Beschta (2003) and D'Elia and Haig (2013) themselves noted that historical data, both pre- and post-European settlement in North America, are often anecdotal, highly imprecise, and narrative in nature, and commonly result in subjective or overly broad estimates of past occurrence or areas of distribution. McKelvey et al. (2008) cautioned that using these types of data may lead to large errors of commission or omission, with significant conservation implications. In some cases, in which anecdotal data provide the only available evidence, researchers must be careful to disclose the likely imprecision of the data set within their work. This may be particularly true when attempting to establish the known range of apex predators such as the grizzly (*U. arctos*) or the jaguar (*P. onca*).

Panthera onca is a species native to the Americas for which few historical data exist in the western United States. The available data, particularly in California, are almost all vague or anecdotal. Nonetheless, Povilitis (2015) stated that recovery, and any subsequent reintroduction or population augmentation of *P. onca* in the United States should be consistent with

historical records, however anecdotal. In other words, despite a very small historical sample size, incomplete and anecdotal data, and/or scant prehistoric evidence, understanding the historic distribution of *P. onca* in California—and the implications of that presence and distribution—should have bearing on any considered reintroduction of this top predator. To further explore the case for reintroducing *P. onca* into previously occupied territory, I reviewed historical records and paleontological evidence to augment the known natural history of *P. onca* in western North America and provide additional data to gauge whether reintroductions may be appropriate.

I conducted a search of the available online and archival documents, reports, journals, and other publications, searching *Panthera onca*, panther, jaguar, *onca*, leopard, spotted, and large cat. Search terms, and numerous combinations associated with California, Arizona, western United States, Alta California, and Baja California were used to identify relevant documents. I reviewed more than 32,000 pages from United States and California State archives on trapping, fur trading, exportation of animal products, and related fields for any report or mention of *P. onca* and associated search terms. Thirty-one books and personal journals (1856–1955), 51 scientific journals, 19 journals associated with the Spanish Missionaries in California, and 94 articles of gray literature were also carefully reviewed. One hundred eighty-six North American-based and 17 international museums of natural history, archeology, and paleontology were queried in the course of this research.

The prehistoric range of *P. onca* in North America has long been a matter of conjecture (Simpson 1941; Dagget and Henning 1974; Seymour 1989). There is relative accord among inferred range maps, which appear to derive from Simpson (1941). All include areas south of Spokane, Washington; eastward towards north central Nebraska; south towards northern Arkansas and central Tennessee; and northeast towards southeast Pennsylvania. This area would inferentially include all of California, however the past range of *P. onca* within present-day California *per se* is unclear and without consensus. Seymour (1989) suggested an area from approximately Santa Barbara County south to the border with Mexico. Hall and Kelson (1959) were more specific, including only the central core of the area suggested by Seymour (1989); their proposed range included the Tehachapi Range and eastern Mojave Desert southward, as well as the Colorado River drainage south of Nevada. When accounts of *P. onca* or similar predatory cats were encountered in conducting this research, I collected the entire excerpt of the account and/or recorded the museum data point, location, collector, and any other associated information that could be used to determine or verify the reported location. If precise, these data were entered on a map (i.e., dot); if imprecise, the data were converted to a shaded area on the map (Fig. 1). Combined, these data produced a hypothetical area of past *P. onca* occupation within California or immediately adjacent (the border regions of Arizona and Mexico). Currently available data suggest at least four areas in which *P. onca* were observed or for which anecdotal evidence suggests that the species was in the immediate area. These accounts were summarized by Merriam (1919), and an additional account was reported by Strong (1926), who claimed a *P. onca* had been killed in California *circa* 1860 (Fig. 1; Table 1). In the time since the reports by Merriam (1919) and Strong (1926), additional direct, verifiable evidence (i.e., bones) of *P. onca* in California has been collected from various sites, including Rancho La Brea in Los Angeles County, California (Jefferson 1983; 1991) (Table 1). The preponderance of evidence has been attributed to the Irvingtonian North American Land Mammal Age (LMA), approximately 0.25–1.6 million years Before Current Era (BCE), and represents fossil animals from that period. An additional *P. onca* fossil reported from Anza-Borrego Desert State Park in Southern California by Jefferson and

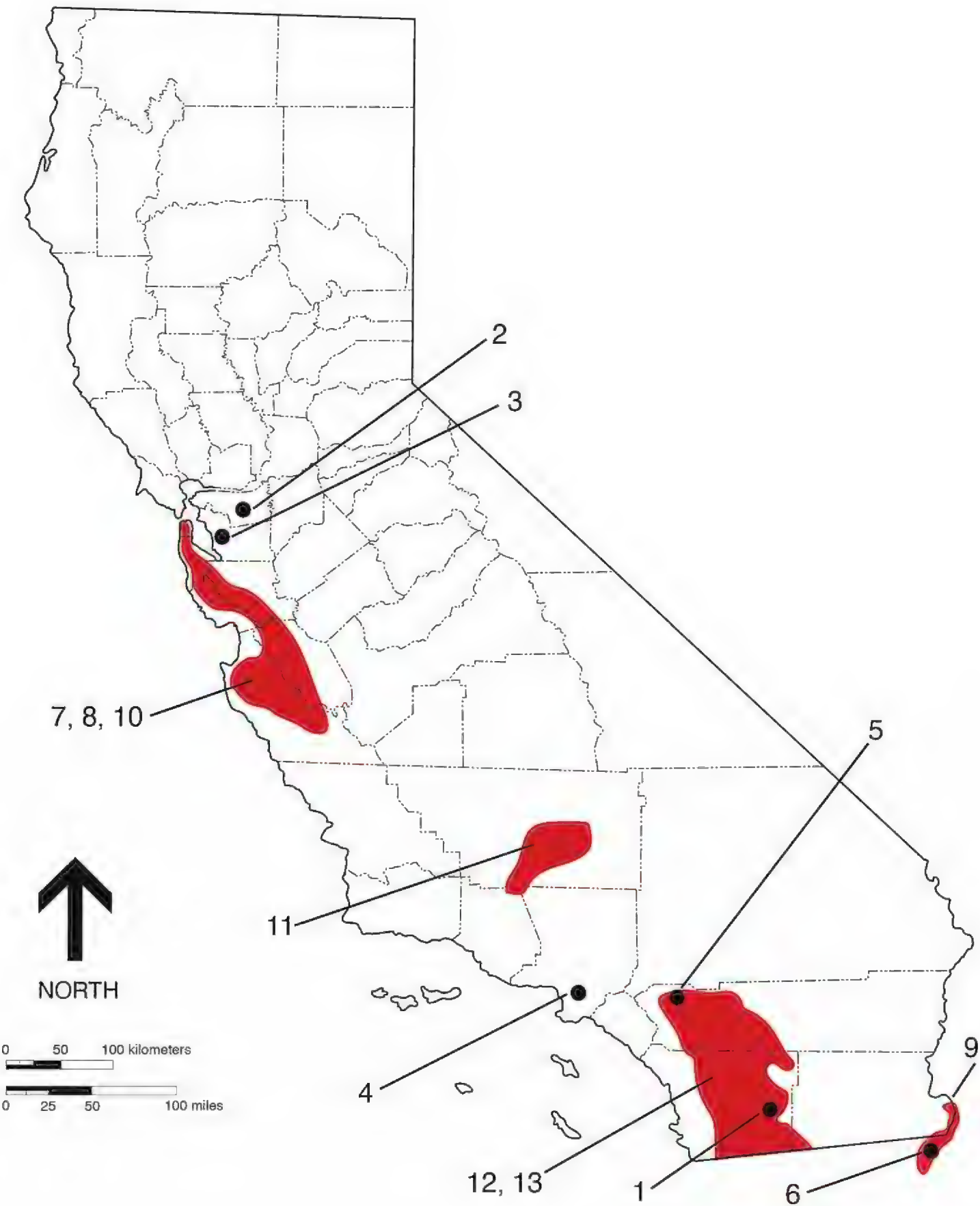


Fig. 1. Locations (dark dots) of prehistoric materials identified as *Panthera onca*, and general locations (red shade) of reported observations of *P. onca* in California from anecdotal reports. Numbers are associated with Table 1 details.

Lindsay (2006) was attributed to the Blancan North American LMA, approx. 4.75–1.6 million years BCE.

The accounts reported by Merriam (1919) and Strong (1926) suggest an area that exceeds that proposed by Seymour (1989) (and therefore also Hall and Kelson [1959]). These 1919 and 1926 accounts proposed an area from northern San Francisco County, southward; a discrete area in the Tehachapi Mountains; a second discrete range similar to that reported by Hall

Table 1. Prehistoric and historical accounts of jaguar (*Panthera onca*) in California. UCMP: University of California Museum of Paleontology, Berkeley, California; PBDB: Paleobiology Database. First-column numbers relate to locations shown in Fig. 1, below.

Specimen		Age/Year	Location	Source
Prehistoric				
1	<i>Panthera onca</i> fossil	Blancan Land Mammal Age	Anza-Borrego State Park, San Diego County	Jefferson and Lindsay 2006
2	<i>P. onca</i> fossil	Irvingtonian LMA	Tassajara, Alameda County	UCMP 130468, 27308
3	<i>P. onca</i> fossil	Irvingtonian LMA	Fremont, Alameda County	UCMP 71237
4	<i>P. onca</i> fossil	Irvingtonian LMA	Rancho La Brea, Los Angeles County	Jefferson 1983, 1991
5	<i>P. onca</i> fossil	Irvingtonian LMA	Fort Irwin, San Bernardino County	PBDB 20335
6	<i>P. onca</i> fossil	Irvingtonian LMA	Colorado River Valley, Mexico	Arroyo-Cabrales 2002, Ruiz-Ramoni 2020
Historical				
7	<i>P. onca</i>	ca 1814	Monterey County area	Von Langsdorff 1814
8	<i>P. onca</i>	1826	San Francisco to Monterey	Beechey 1831
9	<i>P. onca</i>	mid-December 1827	Colorado River, Imperial County	Pattie 1831
10	<i>P. onca</i>	ca 1854	Presidio, San Francisco County	de Saint-Aman 1854
11	<i>P. onca</i>	ca 1860	Tehachapi Mountains, Transverse Range	Hittell 1860
12	<i>P. onca</i>	ca 1860	San Jacinto Mountains, San Bernardino County, and Santa Rosa Mountains, San Diego County	Strong 1926
13	<i>P. onca</i>	1800s (Year Unk)	Cuyamaca Mountains, San Diego County	Merriam 1919

Table 2. Excerpts of accounts from which observations of jaguar (*Panthera onca*) in California were inferred.

Excerpt	Source
“The American lion, <i>Felis concolor</i> , and the American tiger, <i>Felis onca</i> , stags, roes, wolves, foxes, bears, and pole-cats, <i>viverra putorius</i> , are very common here; the latter is called by the Spaniards <i>sorrillo</i> .”	Von Langsdorff 1814
“The lion (<i>Felis concolor</i>) and the tiger (<i>Felis onca</i>) are natives of these woods [the area around Mission San Juan Bautista] but we never saw them; inhabitants say they are small, and the lion is less than the tiger, but more powerful.”	Beechey 1831
“Of birds there are great numbers, and many varieties, most of which I have never before seen. We killed some wild geese and pelicans, and likewise an animal not unlike the African leopard , which came into our camp while we were at work upon a canoe. It was the first we had ever seen.”	Pattie 1831
“There is also the American tiger in California, which is a jaguar . It lives in remote areas, and I have never had the opportunity to meet one. It is said to be more formidable than the cougar. Like him, he climbs trees. A French doctor (Jones) I knew found one in the Presidio, which almost devoured his dog. The Jaguar can carry a horse and an ox very long distances. It is mainly at night that it seeks its prey and makes its victims.”	de Saint-Aman 1854 (translated from the French)
“Barely were my eyes closed, however, when a roar roused me and I started up and strained my eyes along the trail from the den to the trap, but could see nothing. In a few minutes the roar repeated, but in an apparently subdued tone; and directing my eyes in the direction from which it proceeded, I saw a spotted animal, resembling a tiger in size and form , with two young ones.”	Hittell 1860
“...The male beast, as nearly as I could see, was twice as large as an ordinary cougar, and appeared to be covered with dark round spots of great richness and beauty.”	
“...If they were not jaguars , which had strayed up beyond the usual range, I know not what to call them.”	
“Still another bit of evidence comes from Indian tribes of Southern California. An old chief of the Kammei tribe (called by the Spanish ‘Diegenos’) told me the Cuyamaca Mountains region of San Diego County, the ‘ Tiger ’, while rare, was well known to the old Indians, who called it the ‘ Big-spotted Lion ’, Hut’té’kul’ ”.	Merriam 1919
“Francisco Nombre, an old clan chief of the Desert Cahuilla near Coachella, stated that in his youth an animal called tu’kwut, described as a large cat with yellow brown skin marked with spots and having a long tail , was well known in the mountains bordering the desert.”	Strong 1926
“...The last animal of this species he remembers, was killed back of Palm Springs about 1860, by an Indian stalking deer with a deer head disguise. The jaguar attacked the man and was killed by a musket ball. Francisco saw the fresh spotted hide and the long claws which were used as a dog collar.”	

and Kelson (1959) but shifted westward and expanded; and a fourth area comprising the Colorado River drainage between Arizona and California as well as portions of the river basin where it passes through Mexico (Fig. 1). Although it is conceivable that these four disjunct areas were in fact all connected at one time, constituting a range that included the South Coast

Range, the Tehachapi Mountains, the Peninsular Range of Southern California, and portions of the Imperial Valley and Colorado River drainages, no direct or indirect evidence suggests that this was a contiguous range.

Species reintroduction has gained some momentum in California, with current discussions related to reintroduction of grizzly bear (*U. arctos horribilis*), wolverine (*Gulo gulo*), and gray wolf (*C. lupus*) (Alagona 2013; Carroll et al. 2001; Lee et al. 2021). Although recent movements to reintroduce *P. onca* into its former range in the United States (Povilitis 2015; Sanderson et al. 2021) have not yet taken shape, discussion is increasingly likely to surface. Povilitis (2015) and Sanderson et al. (2021) concluded that reintroductions of *P. onca* should be considered as part of the recovery of the species, particularly in a region of Central Arizona, approximately 50 km from the California border. Although the USFWS has no current plans for reintroductions, support for rewilding carnivores is growing worldwide (Wolf and Ripple 2018). Augmentation of carnivore populations has been reported to be more publicly acceptable (Merrill 1999; Cassidy 2024), and may therefore be more likely to be considered for this species, particularly for Arizona and New Mexico, where the species is extant. Additionally, reports of *P. onca* in neighboring Arizona are on the increase, suggesting a potential future dispersal into California (McCain and Childs 2008).

Population growth of gray wolves (*C. lupus*) in the Pacific Northwest over the last two decades was likely the catalyst for natural recolonization of the species in California by individuals migrating from Oregon (Kovacs et al. 2016; Nickel and Walther 2019). In similar fashion, if *P. onca* continues to expand its range in Arizona, or if individuals from Mexico continue to disperse northward, we may well see migration of *P. onca* into California. Additionally, using a spatial prediction model, Jędrzejewski et al. (2018) have suggested a potential viable range that includes portions of Imperial, Orange, Riverside, and San Diego Counties, as well as the Colorado River Delta in Mexico, and reported a probability of future occurrence of up to 75%. Torres (2021) agreed with this potential range but extended it farther eastward into San Diego County and northward through Los Angeles and Ventura Counties. Furthermore, in 2018 the United States Fish and Wildlife Service (USFWS) provided modeling data suggesting the potential for measurable carrying capacities of available *P. onca* habitat that included southeast California.

Recolonization potential for top predators is not unknown for California. *Canis lupus* is well established, through ongoing immigration from Oregon, and at least two separate *Gulo gulo* individuals immigrated into California from other states (Moriarty et al. 2009; Kovacs et al. 2016). These successes may become relevant for *P. onca*, as it has been reported to disperse long distances. Leopold (1959) reported a *P. onca* in northern Baja California (San Pedro Martír, Mexico) that travelled at least 800 km. De la Torre and Rivero (2019) reported that jaguars in Mexico were capable of traveling up to 11 km per day. The nearest observation of *P. onca* to California comes from the Tumacacori Mountains, a range in Santa Cruz and Pima Counties in southern Arizona approximately 230 km southeast of the California border (Warshall 2013); a distance easily comparable to dispersal distances for *P. onca* coming from Mexico.

Ecological, physical, and existential barriers to migration from Arizona into California do exist, including (1) very low numbers of *P. onca* in Arizona (Brown and López-González 2001); (2) the physical barrier of the Colorado River between Arizona and California; and (3) recently erected sections of border wall along the United States-Mexico border. Nevertheless, it can be speculated that at least two of these obstacles could be overcome by migrating *P. onca*. First, Arizona populations may increase over time and produce enough offspring that

one or more individuals are able to move westward and cross into California, and second, given that *P. onca* is a highly proficient swimmer (Da Silveira et al. 2010), crossing the Colorado River would not likely be a true barrier. Undeniably, however, immense sections of the border between the United States and Mexico have been made impermeable by erection of the border wall; only small sections remain open in California and Arizona (Abhat 2011; pers. obs.). If completed, this wall may indeed prove the ultimate barrier to movement of *P. onca* (and other wildlife) across the border. It would take political will and public support to defeat plans for a continuous impenetrable barrier between the two countries.

Although predictive models by Jędrzejewski et al. (2018) and Torres (2021) suggest the possibility of natural recolonization, artificial reintroductions of *P. onca* should not be considered without extensive public input, habitat evaluation, a well-considered management plan, and proactive elevation of the species to endangered status under the California Endangered Species Act (Baker et al. 2017; Maehr et al. 2001; Clark et al. 2005; Sanderson et al. 2021). Reintroductions prompted by public opinion alone are not advisable. In order to be self-sustaining, *P. onca* requires large tracks of relatively undisturbed land (Seymour 1989; USFWS 2018). If the predictive models are accurate, *P. onca* would likely find suitable habitat in an area of California already populated by nearly 20 million people (https://www.california-demographics.com/counties_by_population). Such environments could reduce the availability of prey and compromise the safety of humans and their activities. Although attacks by *P. onca* on humans are very rare ($N = 28$ recorded in history), particularly in the wild ($N = 6$; Neto 2011; Iserson and Francis 2015), large predators can pose a threat to the public and to livestock and pets—interactions that, often as not, result in the precautionary or fear-driven killing of the animal by resource agencies or members of the public (Beier 1991; Carbyn 1989; Ferretti et al. 2015; Herrero et al. 2011).

Warshall (2013) suggested that female *P. onca* migration into Arizona might take 60 to 85 yr, which would push the species' natural establishment in California well into the future—at which time human settlement will presumably have grown significantly. Nevertheless, as mentioned above, a relatively high probability of recolonization of *P. onca* in California does exist (Jędrzejewski et al. 2018; Torres 2021), and State resource agencies should consider the species as potentially occurring naturally at some time in the distant future. Should this come to pass, or if human reintroduction of *P. onca* into California moves ahead after careful consideration of the risks and benefits discussed above, the species will logically warrant emergency listing as endangered, to accord colonizing individuals the greatest chance for survival (Quigley et al. 2017). It is incumbent on us to pave the way for species recolonization with care and deliberation.

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Observation of a Novel Breeding Habitat for the California Red-Legged Frog (*Rana draytonii*) in San Benito County, California

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The California red-legged frog (*Rana draytonii*) is a native ranid that ranges in California from Mendocino and Butte Counties in the north to San Diego County in the south; isolated populations also exist in Baja California (Thomson et al. 2016). This species has been classified as federally Threatened since 1996 (USFWS 2003). *Rana draytonii* is a biphasic amphibian that requires its eggs to be oviposited in perennial and ephemeral aquatic habitat features (Storer 1925; Alvarez et al. 2013a), and whose larvae then metamorphose to become largely terrestrial (Allaback 2010; Tatarian 2008). *Rana draytonii* typically oviposits during the winter in perennial and ephemeral creeks and ponds (Storer 1925; Alvarez et al. 2013a). Several studies exist on the aquatic habitat and microhabitat use by this species for oviposition (Reis 1999; Cook and Jennings 2007; Rathbun 2012; Alvarez et al. 2013a, 2013b; Wilcox et al. 2017; Alvarez and Wilcox 2022). *Rana draytonii* has been reported to reproduce in freshwater creeks and ponds—typically cattle stock ponds (Storer 1925; Fisher and Shaffer 1996; Alvarez et al. 2013a). It is also known to oviposit in brackish water lagoons, such as Abbott’s Lagoon in Point Reyes National Seashore (J. Alvarez pers. obs.), and recent reports indicate widespread use of anthropogenic spring boxes, primarily as non-breeding sites, but occasionally for breeding as well (Alvarez and Wilcox 2022). *Rana draytonii* has been reported to be extirpated from the Central Valley of California, with excessive land disturbance and agricultural cultivation being the chief reasons for its extirpation (Jennings and Hayes 1994). This species is not believed to utilize areas of intense agricultural use (Jennings and Hayes 1994; Fisher and Shaffer 1996) and has not been reported to reproduce in areas such as agricultural ditches and canals. Here we detail the first published record of *R. draytonii* reproducing in an anthropogenic agricultural drainage ditch.

Our observations were made adjacent to an existing site which was immediately adjacent to the intersection of The Alameda Street and Mission Vineyard Road along State Route 156 (36.835861, -121.531646, elev. 71 m), in San Juan Bautista, San Benito County, California, in the South Coast Range. This site is within the known range of *R. draytonii* and was being mechanically denuded of vegetation ahead of anticipated ground disturbance for a State road widening project (Fig.1). The agricultural ditch, called East Ditch, was an open trapezoidal-shaped trench measuring between 2.5–3.0 m wide across the flat bottom, 4.5–6.0 m wide across the top, and was between 1.2–1.8 m deep along its entire length. The site was largely disturbed by long-term and historic agricultural uses and intermixed with relatively natural landscape components including coast redwood (*Sequoia sempervirens*), blue gum eucalyptus (*Eucalyptus globulus*), watercress (*Nasturtium officinale*), poison hemlock (*Conium maculatum*), cattails (*Typha* sp.), fat hen (*Atriplex prostrata*), field bindweed (*Convolvulus arvensis*),

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Fig. 1. Habitat conditions associated with the drainage ditch in San Benito County, California, 27 February 2023. Photograph by Crecencia Sanchez and Rachel Perpignani.

rabbitfoot grass (*Polypogon monspeliensis*), alkali heliotrope (*Heliotropium curassavicum*), non-native slender oat (*Avena barbata*), and poison oak (*Toxicodendron diversilobum*). An agricultural drainage ditch also lay within the site, adjacent to an agricultural plot. This drainage ditch flowed in the direction of San Juan Creek on the westernmost side of the project site. Approximately 0.56 km of the agricultural drainage ditch lay in the project boundaries and was surveyed as part of an investigation to assess wildlife use of the site.

While surveying the drainage for nesting birds on 23 August 2022, we observed one *R. draytonii* larva (Fig. 2). The following evening, we conducted a nighttime survey using 400-lumen flashlights to evaluate *R. draytonii* occupancy on the site. During this survey, we identified two adult and 11 larval *R. draytonii*. Between this survey and 9 September 2022, we relocated approximately 33 larvae, 161 metamorphs, and 7 adults from the site as part of required biological compliance monitoring. On the morning of 27 February 2023, we discovered four spherical amphibian egg mass approximately 10-15 cm in diameter and with several visible larvae resting on its surface (Fig. 3). As we progressed along the drainage ditch, we photographed a total of four egg masses and collected GPS coordinates at each location. The egg masses were identified as that of *R. draytonii* based on their size, the time of year, color of the embryos, and a review of all known amphibians in the area. All four egg masses were attached to dead vegetation and resting near the surface of the water, which was approximately 10-20 cm deep (sensu Alvarez et al. 2013a). Following our observations in February 2023, a significant rain event (1.7 cm) occurred, which altered the conditions of the drainage ditch. Follow-up surveys resulted in no observation of *R. draytonii* eggs and



Fig. 2. Larval *Rana draytonii* in a drainage ditch in San Benito County, California, 23 August 2022. Photograph by Shawn Wagoner.

larvae, and we speculate that a pulse flow washed egg masses and larvae outside of the project area.

Our observations suggest that all life history stages of *R. draytonii* can successfully inhabit and oviposit within agricultural drainage ditches. We found *R. draytonii* over a two-year period in all aquatic and terrestrial life stages. We speculate that these life history stages may be supported, at this site, by ephemeral or nearly ephemeral water, relative disturbance free habitat (i.e., adjacent habitat is heavily disturbed but aquatic habitat is consistent), a lack of non-native fish species (i.e., aquatic predators), and other conditions not noted during our brief period of observation. Moreover, our observation of free-swimming larvae suggests that this novel habitat is suitable for development of egg masses and hatching of larvae. Agricultural drainage ditches are subject to sudden, dramatic changes in water flow rates and volume, and likely contain high concentrations of herbicides and pesticides. The potential



Fig. 3. One of four *Rana draytonii* egg masses, in situ, in a drainage ditch in San Benito County, California, 27 February 2023. Photograph by Crecencia Sanchez and Rachel Perpignani.

consequences of these variables should be investigated further, as should the extent to which *R. draytonii* utilize anthropogenic agricultural water features for breeding, and whether this native species shows a preference for natural versus anthropogenic habitats. Investigating these questions will be critical for addressing the conservation needs of *R. draytonii*. Based on these observations of adults, post-metamorphic frogs, larvae, and egg masses, we conclude that sufficient habitat, in the form of an agricultural drainage ditch, is present for *R. draytonii* at this site, and likely at similar sites elsewhere.

Although no accurate or precise data could be found to report the actual number of kilometers of agricultural ditches that occur within the range of *R. draytonii*, we contend that it is tens of thousands of kilometers. We suggest, that occurrence of *R. draytonii* in agricultural landscapes—a novel habitat for breeding, ovipositing, and hatching larvae—may have far reaching implications for the species management. Further, we suggest that agricultural areas in which *R. draytonii* are present extend hydroperiods of agricultural ditches to mid-summer, to the extent practicable. Additional measures may include investigations into modifications to agricultural ditches, such as the placement of small rock piles, willow trees, or portions of logs that do not hinder agricultural needs but create microhabitat in which egg masses and larvae may be sustained during flash flows.

Our observations suggest two distinct management implications: 1) this habitat type may vastly increase potential habitat used by the species for refuge, foraging, and breeding, and 2) surveys that are conducted to determine the demographic status (i.e., presence/lack of presence) should include agricultural ditches that are in the range of *R. draytonii*.

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An Unusual Nesting Place for California Quail *Callipepla californica*

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California quail *Callipepla californica* inhabit chaparral, woodland, coastal scrub, grassland, semi-desert, brushy areas, parks and farms. They have adapted also to the vicinity of civilization, especially wooded suburbs and neighborhoods with abundant vegetation. They live mostly in family groups and are usually terrestrial, but when disturbed they burst into a fast low flight above the ground. California quail forage on the ground, scratching in the soil and litter, picking up seeds, leaves, fresh shoots, berries, and insects. At night they roost off the ground in tall trees or dense shrubs, often communally above the reach of ground predators (Leopold 1977; National Audubon Society 2024).

Females of California quail typically have one clutch of eggs per year, but they can have two clutches in years with abundant food. Females usually lay 13 or 14 eggs, and then incubate them for 18 to 23 d. They usually nest in an open area, apart from continuous overhead or dense vegetation, and near a source of drinking water. The nest is usually on the ground in a shallow depression lined with leaves and grass, and under cover of a shrub or next to a log. Requisites of good nesting cover are concealment from predators and shade from the sun (Leopold 1977; National Audubon Society 2024).

The downy young of California quail are precocial, leaving the nest within one day after hatching, and they are capable of short flights at age 10 d. Both parents tend the offspring, with the female frequently brooding the young when small and the male keeping vigilance while perched at height. The family remains together as a social group for several months (Leopold 1977; National Audubon Society 2024).

On 3 June 2023, a nesting California quail flushed from a plant pot containing a jade plant *Crassula ovata* (Fig. 1). The homeowner had intended to hide some money among vegetation in the plant pot, when the startled quail flew upward almost into his face. The plant pot was at the front door of the house, 68 m from the urban-wildland interface. It was in a northeast corner of the exterior of the house, shaded from the sun during much of the day, and under cover of the entrance roof. The front door of the house was in frequent use as an entrance/exit by the homeowner, his family and friends.

The plant pot was 71 cm height (including pedestal 2 cm), with outside diameter at the top 44 cm and outside diameter at the bottom 22 cm. The height of the plant above the pot was 35 cm, and widest diameter of the plant was 84 cm. The plant pot contained soil to within 8 cm of its top rim. Inside the plant pot and hidden by the jade plant were at least 16 eggs, lined up in several neat rows and very tight together. The next day two male California quail were observed in the front yard and often near the plant pot, while the female quail was observed sitting on the eggs in the plant pot. Unlike many homes in the neighborhood, the homeowner had no domestic animals (cats or dogs) at his house.

The eggs hatched on 24 June 2023, when at least 12 baby California quail were seen in the nest. One male quail was observed patrolling in circles around the patio at the front of the

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Fig. 1. Top: Plant pot (71 cm height) containing a jade plant *Crassula ovata* and at front door of house, in which a California quail *Callipepla californica* has nested, Ventura, California, 5 June 2023. Bottom: Female California quail sitting on at least 16 eggs in plant pot. The plant pot is 68 m from the urban-wildland interface.

house throughout the day. The next day the family of quail was observed across the street on a property with dense vegetation and abundant leaf litter, and with an absence of domestic animals. In the subsequent days, the male quail was observed frequently standing atop a tall shrub as a sentinel lookout while the family foraged nearby. It is not known how many of the quail chicks survived. The adjacent resident owned a dog and cat, the latter often seen hunting birds where the quail foraged.

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